1982 ✓ (223)

Bioscience Reports 2, 265-276 (1982)
Printed in Great Britain

Article has been made available by the National Library of Medicine and may be protected by copyright under Title 17, U.S. Code

Some effects of disconnecting the cerebral hemispheres

Nobel Lecture, 8 December 1981

Roger SPERRY

Division of Biology, California Institute of Technology, Pasadena, California 91125, U.S.A.

Introduction: Classic View of Cerebral Dominance

To start by looking back a little, recall that even a small brain lesion, if critically located in the left or language hemisphere, may selectively destroy a person's ability to read, while at the same time sparing speech and the ability to converse. The printed page continues to be seen, but the words have lost their meaning. This condition typically follows from focal damage to the angular gyrus in the left hemisphere. It also results from lesions interrupting the neural input to this left angular gyrus from the visual or calcarine cortical areas (1,2). It is natural to conclude in such cases that the left hemisphere is responsible for reading while the undamaged right hemisphere, in contrast, must be 'word-blind' or incapable of seeing meaning in the printed word.

The same applies with respect to the capacity to comprehend *spoken* words. Focal lesions within Wernicke's area near the base of the left temporal lobe, or again, lesions that disconnect this area from its input arriving from the auditory receiving centers of the cortex have been shown to regularly abolish the capacity to understand spoken language (2). Speech continues to be heard but the meaning is lost. Again, such cases seem to tell us that word comprehension is confined to the left hemisphere and that the spared right hemisphere must be word-deaf, as well as word-blind.

The accumulation of many observations of this kind where left, but not right, focal damage destroys the comprehension, as well as the expression, of language helped to give rise over the years to the so-called classic view in neurology of a dominant or major, left, language hemisphere and a subordinate, or minor, nonlanguage hemisphere. The minor hemisphere in addition to being unable to talk, and unable to write, and word-deaf and word-blind, was inferred by extrapolation to be typically lacking also in the higher cognitive faculties associated with language and symbolic processing.

This classic view of cerebral dominance was further reinforced by parallel findings on apraxia in which disorders of learned volitional movement were reported to follow predominantly lesions on the left side. The left hemisphere accordingly came to be regarded as being also the leading motor executive for the direction and control of higher volitional movements and the major repository for the cerebral engrams of motor learning (3,4). Evidence for left dominance extended further to calculation and arithmetic reasoning (5). Thus, with few exceptions, the bulk of the collected lesion evidence up through the 1950s into the early '60s converged to support the picture

© *The Nobel Foundation 1982*

of a leading, more highly evolved and intellectual left hemisphere and a relatively retarded right hemisphere that by contrast, in the typical righthander brain, is not only mute and agraphic but also dyslexic, word-deaf, and apraxic, and lacking generally in higher cognitive function.

Contrasting Evidence from Commissurotomy

It thus came as a considerable surprise in the early 1960s when tests on commissurotomy or 'split-brain' patients seemed to indicate the presence in the right, so-called 'minor' hemisphere of a considerable capacity for cognitive understanding and the comprehension of language, both written and spoken. These were patients of the neurosurgeons Joseph Bogen and his chief, Phillip Vogel of the White Memorial Medical Center in Los Angeles. The patients had undergone a midline surgical section of the corpus callosum and other forebrain commissures in a last-resort effort to control severe, intractable epilepsy. The operation severed all neural cross connections for direct communication between the two hemispheres. From experience with this operation in human patients (6) and from nearly 10 years of split-brain animal studies (7), it could be predicted that the effect would not be seriously incapacitating as far as ordinary daily activities were concerned, and this proved to be the case. Given six months to a year for recovery and in the absence of other major brain pathology, a person with complete section of the forebrain commissures would go undetected as a rule in a casual first meeting or conversation or even through an entire routine medical exam.

Our early studies with Michael Gazzaniga (8-10) on these patients seemed to show from the start that the disconnected right hemisphere was by no means word-deaf as anticipated, nor either word-blind. Lateralized testing for linguistic abilities showed the right hemisphere to be largely mute and agraphic, but nevertheless able to comprehend, at a moderately high level, words spoken aloud by the examiner. The disconnected right hemisphere also was able to read printed words flashed to the left visual field - as demonstrated manually in each case by selective retrieval or by pointing to corresponding objects or pictures in a choice array. The commissurotomy patients were also able with the right hemisphere to choose correct written or spoken words to match presented objects or pictures and to go correctly from spoken to printed words and vice versa. Correct tactual retrieval by the right hemisphere was achieved for objects not directly named but only described with complex spoken phrases like 'a measuring instrument', 'container for liquids', etc. With the disconnected right hemisphere, these patients could also spell three- and four-letter words with cutout letters and could read such words presented tactually. These linguistic capabilities of the right hemisphere have more recently been affirmed and extended in a comprehensive series of experiments by Zaidel (11) using his improved scleral lens technique that allows prolonged viewing. So strong was contemporary neurological doctrine to the contrary in the early sixties that Dr. Bogen felt obliged in good conscience to withdraw his name from our initial papers on language.

Our own conviction that the answers on these language tests had to be coming from the right and not from the left half of the brain was based on lateralized testing procedures in which the speaking left hemisphere could be shown, by follow-up verbal questions, to have remained incognizant or quite unaware of the answers and performances being ascribed to the right hemisphere. Each disconnected hemisphere behaved as if it were not conscious of cognitive events in the partner hemisphere - just as had been the case in our split-brain animal studies of the 1950s, started by Ronald Myers (12) at the University of Chicago. Each brain half, in other words, appeared to have its own, largely separate, cognitive domain with its own private perceptual, learning, and memory experiences, all of which were seemingly oblivious of corresponding events in the other hemisphere. Although the basic hemisphere deconnection syndrome in man (10) proved to be essentially similar to that worked out earlier in cats and monkeys, its manifestation was much more dramatic in the human subjects. The speaking hemisphere in these patients could tell us directly in its own words that it knew nothing of the inner experience involved in test performances correctly carried out by the mute partner hemisphere. Lateralization of brain functions could be inferred, not only from the deficiency or absence of function on one side but also from its concurrent presence on the other.

Right-Hemisphere Language Controversy

The unexpected language capacities found in the right hemisphere after commissurotomy posed some controversial issues the answers to which are still not entirely resolved. Very simply, the problem raised is the following: Why is it that the right hemisphere is able to do things following commissurotomy, such as reading, that it fails to do in the presence of focal damage in the left hemisphere? It has been suggested in answer (13-15) that the commissurotomy evidence may be misleading because of an atypical bilateral spread of language into the right hemisphere correlated with the long-term epilepsy and associated pathology. A further criticism has invoked individual variation in view of the small patient group involved.

We have favored another interpretation which suggests conversely that it is the unilateral lesion evidence that has been misleading. The reasoning here says that left lesions in the presence of the commissures act to prevent the expression of latent function, actually present but suppressed, within the undamaged right hemisphere (10). This interpretation assumes that the two halves of the brain, when connected, work closely together as a functional unit with the leading control being in one or the other. When this unitary function is rendered defective by a one-sided lesion, the resultant impaired function prevails with respect to both hemispheres. That is, the two continue to operate as an integral, though defective, functional unit. Only after the intact right hemisphere is released from its integration with the disruptive and suppressive influence of the damaged hemisphere, as effected by commissurotomy, can its own residual function become effective.

This interpretation found support also in the limited hemispherectomy data available (16). The same reasoning has seemed to apply

as well to phenomena of unilateral neglect and apraxia, neither of which proved to be nearly so severe in lateralized tests after commissurotomy as one might have expected from the lateral lesion findings. Although the final word on these various issues is not yet in, the foregoing interpretation has received considerable support in subsequent commissurotomy studies which reveal the presence in the disconnected right hemisphere of additional superior cognitive capacities that can hardly be ascribed either to an atypical bilateralization of language or, any longer, to individual variation. There is reason to think that these other faculties also had gone unrecognized because of complexities that inevitably prevail in the presence of the commissures.

Right-Hemisphere Specialization

Earlier indications of right-hemisphere specialization in the lateral-lesion data, such as in facial recognition, dressing, making block designs, drawing three-dimensional cubes, etc., had been ascribed to asymmetry in the sensory and motor-executive realms primarily rather than in higher central cognitive levels. These right-hemisphere functions were referred to as 'visuospatial', 'constructional', or 'praxic'. In keeping with conventional conceptions of cerebral dominance, any higher cognitive processing that might be involved in such activities could be assumed to be contributed from the left hemisphere via the commissures. Our own initial interpretations of these activities did not depart substantially from the classic view (17).

By 1967, however, the collected observations on the commissurotomy subjects were being taken to uphold the conclusion (18) that each of the disconnected hemispheres, not only the left, has its own higher gnostic functions. Each hemisphere in the lateralized testing procedures appeared to be using its own percepts, mental images, associations, and ideas. As in the split-brain animal studies, each could be shown to have its own learning processes and its own separate chain of memories, all, of course, essentially inaccessible to conscious experience of the other hemisphere.

Added evidence for involvement of the right hemisphere in higher intellectual processing came from study of a case of congenital absence of the corpus callosum with an above-average verbal IQ and in whom speech was found to be present in the right as well as the left hemisphere (19,20). The scholastic records of this college student with callosal agenesis were fair to good for courses that involved language and verbal facility, but contrastingly poor for subjects such as geometry and geography that involved spatial and related nonverbal faculties which we now commonly associate with the right hemisphere. The extra language in the right hemisphere had apparently been attained at the expense of the usual nonverbal cognitive faculties that otherwise normally develop there.

More direct, controlled evidence for right-hemisphere superiority in tasks requiring higher cognitive ability came from studies by Jerre Levy (21,22) aimed specifically at cognitive specialities of the right hemisphere. She found that the mental capacity to make intermodal spatial transformations from three-dimensional to unfolded, two-

dimensional forms was much better developed in the right hemisphere. Also where items in the test series showed higher scores by the left hemisphere there was a corresponding drop in right-hemisphere performance suggesting a left-right polarity in cognitive abilities.

From these data, taken in conjunction with available clues from the literature, Levy proposed that left and right hemispheres are characterized by inbuilt, qualitatively different and mutually antagonistic modes of cognitive processing, the left being basically analytic and sequential, the right spatial and synthetic. A rationale was added for the evolution of cerebral asymmetry (23) based on the functional advantages of having the two cognitive modes develop in separate hemispheres in order to minimize mutual interference.

In succeeding years thinking evolved rapidly along these lines and became strengthened and refined through a series of studies (24-31) in which it proved possible to demonstrate further that the so-called subordinate or minor hemisphere, which we had formerly supposed to be illiterate and mentally retarded and thought by some authorities to not even be conscious, was found to be in fact the superior cerebral member when it came to performing certain kinds of mental tasks. The right-hemisphere specialities were all, of course, nonverbal, nonmathematical, and nonsequential in nature. They were largely spatial and imagistic, of the kind where a single picture or mental image is worth a thousand words. Examples include reading faces, fitting designs into larger matrices, judging whole circle size from a single arc, discrimination and recall of nondescript shapes, making mental spatial transformations, discriminating musical chords, sorting block sizes and shapes into categories, perceiving wholes from a collection of parts, and the intuitive perception and apprehension of geometrical principles. The emphasis meantime became shifted somewhat from that of an intrinsic antagonism and mutual incompatibility of left and right processing to that of a mutual and supportive complementarity.

In many cases the observed left-right cognitive differences were rather subtle and qualitative in nature, such that they would easily be obscured in lateral-lesion studies by individual variation and background pathology. Under the conditions of commissurotomy where background factors are equalized and where close left-right comparisons become possible within the same subject working the same problem, even slight lateral differences become significant. The same individual can be observed to employ consistently one or the other of two distinct forms of mental approach and strategy, much like two different people, depending on whether the left or right hemisphere is in use.

Further Extensions

Further developments from other sources have advanced in many directions through study of various normal, brain-damaged, and other select populations (32,33), exploring correlations with handedness, gender, occupational preferences and ability, special innate talents, genetic variations like Turner's syndrome, congenital dyslexia, endocrine pathology, autism, dreaming, hypnosis, inverted writing - and others. In some cases the conclusions along with the growing wave of semipopular extrapolations and speculations concerning 'left-brain' vs.

'right-brain' functions call for a word of caution. The left-right dichotomy in cognitive mode is an idea with which it is very easy to run wild. Qualitative shifts in mental control may involve up-down, front-back, or various other organizational changes as well as left-right differences. Furthermore, in the normal state the two hemispheres appear to work closely together as a unit, rather than one being turned on while the other idles. Much yet remains to be settled in all these matters. Even the main idea of differential left and right cognitive modes is still under challenge in some quarters in favor of the view that the right-hemisphere specialities are primarily praxic or 'manipulospatial' in character and that higher cognition and self awareness are associated mainly with language in the left hemisphere (34,35).

Regardless of remaining uncertainties concerning laterality, one beneficial outcome that appears to hold up is an enhanced awareness, in education and elsewhere, of the important role of nonverbal components and forms of intellect. Another positive outcome that derives from evidence involving familial, mutational, sexual and other innate variations is a growing recognition of, and respect for the inherent individuality in the structure of human intellect. The more we learn, the more complex becomes the picture for predictions regarding any one individual and the more it seems to reinforce the conclusion that the kind of unique individuality inherent in our brain networks makes that of fingerprints or facial features appear gross and simple by comparison. The need for educational tests and policy measures to selectively identify, accommodate, and maximize the differentially specialized forms of individual intellectual potential becomes increasingly evident.

Self Consciousness and Social Awareness

Earlier contentions that the right hemisphere is not even conscious largely gave way by the mid seventies to an intermediate position conceding that the mute hemisphere may be conscious at some lower elemental levels, but claiming that it lacks the higher, reflective, self-conscious kind of inner awareness that is special to the human mind and is needed, so it is said, to qualify the right conscious system as a 'self' or 'person' (36,37). Self awareness in particular is reported, on the basis of mirror tests mainly, to be a predominantly human attribute and is rated by developmental as well as evolutionary standards to be a highly advanced phase of conscious awareness.

Accordingly we undertook to test the right hemisphere more specifically for the presence of self recognition and related forms of self and social awareness. With perception of pictorial stimuli confined to one hemisphere by the scleral contact lens occluder developed by Eran Zaidel (38), the subject merely had to point to select items in a multiple choice array in answer to various kinds of leading questions regarding his or her knowledge and feelings concerning the content of the pictures. Subject's responses included also differential emotional expressions, thumbs-up, thumbs-down evaluations, exclamations, and spontaneous remarks relevant to the emotional aspects of affect-laden stimuli.

The results (39) revealed that the disconnected right hemisphere readily recognizes and identifies him or herself among a choice array of portrait photos, and in doing so, generates appropriate emotional reactions and displays a good sense of humor requiring subtle social evaluations. Similar findings were obtained for pictures of the immediate family, relatives, acquaintances, pets, personal belongings, familiar scenes and also political, historical, and religious figures, as well as television and screen personalities. The relatively inaccessible inner world of the nonspeaking hemisphere was thus found to be surprisingly well developed. The general level of performance on these tests was in good accord with that obtained from the left hemisphere of the same subject or in free vision. Results to date suggest the presence of a normal and well-developed sense of self and personal relations along with a surprising knowledgeability in general.

Similar projective procedures were used to explore for a sense of time in the right hemisphere and the presence of concern for the future with thus far no evidence of abnormal deficit. The nonvocal hemisphere appears to be quite cognizant of the person's daily and weekly schedules, the calendar, seasons, and important dates of the year. The right hemisphere also makes appropriate discriminations that show concern with regard to the thought of possible future accidents and personal or family losses. The need for life, fire, and theft insurance, for example, seems to be properly appreciated by the mute hemisphere.

Unlike other aspects of cognitive function, emotions have never been readily confinable to one hemisphere. Though generated by lateralized input, the emotional effects tend to spread rapidly to involve both hemispheres, apparently through crossed fiber systems in the undivided brain stem. In the above tests for self consciousness and social awareness it was found that even subtle shades of emotion or semantic connotations generated in the right hemisphere could be quite helpful to the left hemisphere in its efforts to guess the nature of a stimulus known only to the right hemisphere. The results suggested that this affective, connotational, or semantic component could play an extremely important role in cognitive processing generally.

The more structured and specific informational components of cognitive processing were shown to be separable from the emotional and connotational components. The former remained confined within the hemisphere in which it was generated, whereas the emotional overtones leaked across to influence neural processing in the other hemisphere. The evidence of this separability is in itself significant in regard to questions of the organization of the neural mechanisms of cognition. Also, since the affective component appears to be an eminently conscious property, the fact that it crosses at lower brain-stem levels is of interest in reference to the structural basis of consciousness. A major thrust in our current work is aimed at determining more precisely what shades of emotional, connotational, or semantic content are able to cross through the brain stem and how they affect cognitive processing on the other side. In these studies we are using a new technique just developed for lateralizing vision (40,41). It allows prolonged viewing without any attachments to the eye.

Breakthrough in the Mind-Brain Problem

In closing it remains to mention briefly that one of the more important things to come out of the split-brain work, as an indirect spin-off, is a revised concept of the nature of consciousness and its fundamental relation to brain processing (42-44). The key development here is a switch from prior non-causal, parallelist views to a new causal, or 'interactionist' interpretation that ascribes to inner experience an integral causal control role in brain function and behavior. In effect, and without resorting to dualist views, the mental forces and properties of the conscious mind are restored to the brain of objective science from which they had long been excluded on materialist-behavioralist principles.

Acceptance of the revised 'causal view' and the reasoning involved, now becoming widespread, carries important implications for science and for scientific views of man and nature. Cognitive introspective psychology and related cognitive science can no longer be ignored experimentally, or written off as 'a science of epiphenomena', nor either as something that must, in principle, reduce eventually to neurophysiology. The events of inner experience, as emergent properties of brain processes, become themselves explanatory causal constructs in their own right, interacting at their own level with their own laws and dynamics. The whole world of inner experience (the world of the humanities) long rejected by twentieth-century scientific materialism, becomes recognized and included within the causal domain of science.

Basic revisions in concepts of causality are involved in which the whole, besides being 'different from and greater than the sum of the parts', also causally determines the fate of the parts, without interfering with the physical or chemical laws of the subentities at their own level. It follows that physical science no longer perceives the world to be reducible to quantum mechanics or to any other unifying ultra element or field force. The qualitative, holistic properties at all different levels become causally real in their own form and have to be included in the causal account. Quantum theory on these terms no longer replaces or subsumes classical mechanics but rather just supplements or complements.

The results add up to a fundamental change in what science has long stood for throughout the materialist-behaviorist era (45). The former scope of science, its limitations, world perspectives, views of human nature, and its societal role as an intellectual, cultural, and moral force all undergo profound change. Where there used to be conflict and an irreconcilable chasm between the scientific and the traditional humanistic views of man and the world (46,47), we now perceive a continuum. A unifying new interpretative framework emerges (48) with far-reaching impact not only for science but for those ultimate value-belief guidelines by which mankind has tried to live and find meaning.

Acknowledgements

Our split-brain studies could hardly have succeeded without the contributions of a long line of very able graduate students and postdoctoral associates. I am particularly grateful to Ronald Myers, who started the animal work in his doctoral research at the University of Chicago; Michael Gazzaniga, first to work with the human subjects, and Jerre Levy, first to demonstrate superior cognitive processing in the right hemisphere. All contributed immensely to these respective innovations as did others to more specific aspects of the program. We are deeply indebted to Drs. Joseph Bogen and Phillip Vogel for generously making their patients available to study, and to the patients themselves, without whose long and willing cooperation the human work would not have been possible.

Our work has been dependent for funding since the late 1950s on successive federal grants conferred mainly by the National Institute of Mental Health. My chair at Caltech was made possible and has been sustained throughout by the F. P. Hixon Fund of the California Institute of Technology donated to bring to the Institute research bearing on 'the "why" of human behavior'.

For research assistance in the human studies we owe much to the dedicated efforts of Dahlia Zaidel over a 9-year period beginning in 1967, and to those also of Lois MacBird in both the animal, and more recently, the human work extending over a 25-year period to the present. Our research progress has been dependent in no small measure on the consistent support received on all sides at Caltech. My own efforts could not have prospered without the constant help and understanding of Norma, my wife, whose competence and willingness in handling matters of our home and family has freed me over the years to give added time to problems of the laboratory.

References

1. Greenblatt SH (1977) Neurosurgery and the anatomy of reading: A practical review. Neurosurgery 1, 6-15.
2. Brown JW (1972) *Aphasia, Apraxia and Agnosia; Clinical and Theoretical Aspects,* Charles C. Thomas, Springfield, Illinois.
3. Liepmann H (1906) Der weitere Krankheitsnerlauf bei dem einseitig Apraktischen und der Gehirnbegund auf Grund von Serienschnitten. Monatschrift fur Psychiatrie und Neurologie 19, 217-243.
4. Geschwind N (1975) The apraxias: neural mechanisms of disorders of learned movement. Am. Scient. 63, 188-195.
5. Hecaen H (1962) Clinical symptomatology in right and left hemispheric lesions. In *Interhemispheric Relations and Cerebral Dominance* (Mountcastle VB, ed), pp 215-243, Johns Hopkins, Baltimore.
6. Akelaitis AJ (1944) A study of gnosis, praxis, and language following section of the corpus callosum. J. Neurosurg. 1, 94-102.
7. Sperry RW (1961) Cerebral organization and behavior. Science 133, 1749-1757.
8. Gazzaniga MS & Sperry RW (1967) Language after section of the cerebral commissures. Brain 90 (I), 131-148.
9. Sperry RW & Gazzaniga MS (1967) Language following surgical

disconnection of the hemispheres. In *Brain Mechanisms Underlying Speech and Language* (Millikan CH & Darley FL, eds), pp 177-184, Grune and Stratton, New York.
10. Sperry RW, Gazzaniga MS & Bogen JE (1969) Interhemispheric relationships: the neocortical commissures; syndromes of hemisphere disconnection. In *Handbook of Clinical Neurology* (Vinken PJ & Bruyn GW, eds), vol 4, pp 177-184, North-Holland, Amsterdam.
11. Zaidel E (1978) Lexical structure in the right hemisphere. In *Cerebral Correlates of Conscious Experience* (Buser P & Rougeul-Buser A, eds), Elsevier, Amsterdam.
12. Myers RE (1955) Interocular transfer of pattern discrimination in cats following section of crossed optic fibers. J. Comp. Physiol. Psychol. **48**.
13. Geschwind N (1974) 'Discussion'. In *Les Syndromes de disconnexion calleuse chez l'homme* (Michel F & Schott B, eds), Lyon Hospital Neurologique.
14. Selnes OA (1976) A note on 'On the representation of language in the right hemisphere of right-handed people'. Brain and Language, 583-590.
15. Whitaker HA & Ojemann GA (1977) Lateralization of higher cortical functions: a critique. In *Evolution and Lateralization of the Brain* (Dimond S & Blizard DA, eds), Ann. N. Y. Acad. Sci. **299**, pp 459-473.
16. Smith A (1966) Speech and other functions after left (dominant) hemispherectomy. J. Neurol. Neurosurg. & Psychiat. **29**, 467-471.
17. Bogen JE & Gazzaniga MS (1965) Cerebral commissurotomy in man. Minor hemisphere dominance for certain visuospatial functions. J. Neurosurg. **23**, 394-399.
18. Sperry RW, Vogel PJ & Bogen JE (1970) Syndrome of hemisphere deconnection. In *Proceedings 2nd Pan-Am Congress of Neurology* (Bailey P & Foil RE, eds), pp 195-200, Puerto Rico.
19. Saul R & Sperry RW (1968) Absence of commissurotomy symptoms with agenesis of the corpus callosum. Neurology **18**, 307.
20. Sperry RW (1968) Plasticity of neural maturation. Developmental Biology Supplement **2**, 306-327.
21. Levy J (1970) Information processing and higher psychological functions in the disconnected hemispheres of commissurotomy patients. Unpublished doctoral dissertation, California Institute of Technology (Ann Arbor, Mich.: University Microfilms No. 70-14, 844).
22. Levy-Agresti J & Sperry RW (1968) Differential perceptual capacities in major and minor hemispheres. Proc. Natl. Acad. Sci. U.S.A. **61**, 1151.
23. Levy J (1969) Possible basis for the evolution of lateral specialization of the human brain. Nature **224**, 614-615.
24. Zaidel D & Sperry RW (1973) Performance on the Raven's Colored Progressive Matrices text by subjects with cerebral commissurotomy. Cortex **9**, 34-39.
25. Nebes RD (1971) Superiority of the minor hemisphere in commissurotomized man for the perception of part-whole relations. Cortex **7**, 333-349.

26. Nebes RD (1972) Dominance of the minor hemisphere in commissurotomized man on a test of figural unification. Brain **95**, Part III, 633-638.
27. Gordon HW (1971) Hemispheric asymmetries in the perception of musical cords. Cortex **6**, 387-398.
28. Kumar S (1971) Lateralization of concept-formation in human cerebral hemispheres. *Caltech Biology Annual Report*, No. 136, pp 118-119, California Institute of Technology.
29. Milner B & Laughlin T (1972) Right-hemisphere superiority in tactile pattern-recognization after cerebral commissurotomy: evidence for nonverbal memory. Neuropsychologia **10**, 1-15.
30. Levy J, Trevarthen C & Sperry RW (1972) Perception of bilateral chimeric figures following hemispheric deconnexion. Brain **95**, 61-78.
31. Franco L & Sperry RW (1977) Hemisphere lateralization for cognitive processing of geometry. Neuropsychologia **15**, 107-114.
32. Dimond S & Beaumont JG (eds) (1974) *Hemisphere Function in the Human Brain*, Paul Eleck, London.
33. Dimond ST & Blizard DA (eds) (1977) *Evolution and Lateralization of the Brain*. Ann. N. Y. Acad. Sci. **299**.
34. LeDoux JE, Wilson DH & Gazzaniga MS (1977) Manipulo-spatial aspects of cerebral lateralization: clues to the origin of lateralization. Neuropsychologia **15**, 743-749.
35. Eccles JC (1980) *The Human Psyche* (The Gifford Lectures), Springer-Verlag, Berlin.
36. DeWitt L (1975) Consciousness, mind and self: The implications of the split-brain studies. Brit. J. Philos. Sci. **26**, 41-47.
37. Popper K & Eccles J (1977) *The Self and Its Brain: An Argument for Interactionism*, Springer International, Berlin.
38. Zaidel E (1975) A technique for presenting lateralized visual input with prolonged exposure. Vision Res. **15**, 283-289.
39. Sperry RW, Zaidel E & Zaidel D (1979) Self recognition and social awareness in the deconnected minor hemisphere. Neuropsychologia **17**, 153-166.
40. Sperry RW & Myers JJ (1981) A simplified technique for lateralizing visual input. *Caltech Biology Annual Report*, No. 231.
41. Myers JJ & Sperry RW (1982) A simple technique for lateralizing visual input that allows prolonged viewing. Submitted for publication.
42. Sperry RW (1965) Mind, brain and humanist values. In *New Views of the Nature of Man* (Platt JR, ed), pp 71-92, University of Chicago Press, Chicago.
43. Sperry RW (1969) A modified concept of consciousness. Psychological Review **76**, 532-536.
44. Sperry RW (1980) Mind-brain interaction: mentalism, yes; dualism, no. Neuroscience **5**, 195-206.
45. Sperry RW (1981) Changing priorities. Ann. Rev. Neurosci. **4**, 1-15.
46. Snow CP (1959) *The Two Cultures and the Scientific Revolution*, Cambridge University Press, New York.

47. Jones WT (1965) *The Sciences and the Humanities: Conflict and Reconciliation*, University of California Press, Berkeley and Los Angeles.
48. Sperry RW (1982) *Science and Moral Priority: The Merging of Mind, Brain and Values*, vol 4 of *Convergence* Series, founded by R. N. Anshen, Columbia University Press, New York.

Bioscience Reports 2, 277-287 (1982)
Printed in Great Britain

The predominant surface glycoproteins of thymocytes and lymphocytes

Review

Alan F. WILLIAMS

MRC Cellular Immunology Unit, Sir William Dunn School of Pathology, University of Oxford, Oxford OX1 3RE, U.K.

The surfaces of thymocytes and T and B lymphocytes differ markedly in their predominant glycoprotein constituents. Amino acid sequence studies show that a surprising number of the cell surface molecules have homologies with immunoglobulins. Analysis of carbohydrate shows major differences between glycoproteins on the same cell and between the same (or closely related) glycoproteins on the different cell types.

Introduction

There are two main types of immunocompetent lymphocytes: B lymphocytes, which differentiate in the bone marrow and give rise to antibody-secreting cells, and T lymphocytes, which differentiate in the thymus and are responsible for cell-mediated immunity. The surface molecules of both B and T lymphocytes have been intensively studied and also those of immature T lymphocytes from the thymus (thymocytes). Under the microscope mature B and T lymphocytes and most thymocytes look very similar, with a large nuclear:cytoplasmic ratio, few mitochondria, and an absence of endoplasmic reticulum. These features are consistent with the fact that these are non-dividing cells with low levels of metabolism and biosynthetic activity.

In the absence of antigen, lymphocytes have a migratory existence during which they recirculate from blood to lymph. This involves specific recognition of specialized endothelium in lymph nodes, movement between endothelial cells, and migration into areas which are different for B and T lymphocytes. The time of passage through the nodes is much shorter for T lymphocytes than for B lymphocytes (1). If foreign antigen is encountered a complex set of recognition events occurs. B lymphocytes can bind antigen directly with their immunoglobulin receptors but require interactions with macrophages and T lymphocytes to trigger cell division and differentiation to produce antibody-secreting cells and memory cells (2). T lymphocytes appear to recognize antigen in association with histocompatibility antigen presented on macrophages or dendritic cells. The molecular basis of this is not understood at all (3).

Given the above functions it seems reasonable to think that the cell surface molecules of B and T lymphocytes will be mainly involved with the recognition phenomena seen in recirculation and cell positioning, and antigen recognition. For thymocytes, surface molecules may be involved in cell positioning and in events leading to commitment to a particular specificity of antigen recognition. I would

©1982 The Biochemical Society